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Analysis of the phenotypic link between behavioural traits at mixing and increased long-term social stability in group-housed pigs

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Abstract

Mixing of growing pigs results in aggressive contests between group members. As aggression serves to establish dominance relationships, it is possible that increased initial aggression may facilitate the formation of social hierarchies. The objective of the study was to investigate whether there is a phenotypic link between behavioural traits of aggression at mixing and increased long-term group social stability. Aggressive behavioural traits were recorded for 24 hours after mixing, whereas the numbers of skin lesions (anterior, central and posterior) were obtained 24 hours (SL24h) and 3 weeks post-mixing (SL3wk) for 1,166 pigs. At the group level, aggressive behavioural traits were positively correlated with anterior SL24h (0.34 to 0.67; $P < 0.01$) at mixing, and negatively with central SL3wk (-0.28 to -0.38; $P < 0.01$) in the stable group. At the individual animal level, most behavioural traits of aggressiveness correlated positively with SL24h (0.09 to 0.53; $P < 0.001$), whereas the opposite associations were found for SL3wk (-0.06 to -0.14; $P < 0.05$). Within aggressive cohorts, animals with a high fight success rate received slightly fewer SL24h than equally aggressive, but unsuccessful pen mates, while animals that avoided aggression received the fewest SL24h. Corresponding associations were reversed in the stable group. These results provide evidence that increased aggression at mixing may aid stable hierarchy formation. This raises an ethical dilemma in pigs production, but potentially also in other species, that increased acute aggression during mixing may actually decrease chronic aggression in groups and thus benefit the long term welfare of the group.

Keywords: aggressive behaviour; long-term social behaviour; mixing aggression; pigs, skin lesions

1. Introduction

Repeated mixing of livestock species that adopt social systems characterised by dominance hierarchies disrupts social relationships and results in aggressive contests between group members. This kind of aggressive behaviour serves to establish dominance hierarchies (Meese & Ewbank, 1973) but may be associated with high stress and injury levels, especially in pigs, where the costs of aggression can be particularly significant. These effects make social aggression a known welfare and economic concern in pig production, affecting growth, reproduction, and carcase quality (Faucitano, 2001; Marchant et al., 1995; Stookey & Gonyou, 1994). As well as the physical and metabolic demands of prolonged fighting, an uncertain hierarchy position may be stressful to individuals (DeVries et al., 2003). In pigs, individuals that were involved in aggression upon mixing but only achieved moderate fight success have been shown to have higher baseline salivary cortisol levels than bottom and top ranking group members (Coutellier et al., 2007; Mendl et al., 1992) implying that these animals may feel more stressed than their subordinates. Methods of reducing aggression have been studied for over 30 years (Fraser 1984); however to date no practical, socially acceptable, low cost, high impact solution has been found.

Physical aggression between pigs can cause injuries in the form of skin lesions. Lesions to the anterior and central regions of the body have been shown to correspond with the duration of reciprocal fighting, while lesions to the posterior region of the body are associated with the receipt of non-reciprocal bullying (Turner et al., 2006[a]). The number of lesions has been found to moderately correlate with the duration of time spent engaged in aggression, and combining the location and number of skin lesions has been shown to be a useful proxy measure of aggression (Turner et al., 2006[a]).

In commercial farming, once pigs are mixed for growing they will usually remain in these groups for several months until regrouped again or marketed. As aggression serves to establish dominance hierarchies, it is possible that increased aggression upon first mixing may actually lead to more stable dominance relationships in the long-term. Indeed, there is some evidence that initial increased aggression at mixing results in lower aggression and improved productivity over the entire growing-finishing period (Canario et al., 2012; D'Eath, 2005; Turner et al., 2009). If this is the case, aggressiveness at mixing would be essential to improved long term welfare and production.

Efforts to reduce aggression in commercial pigs either through different management strategies, environmental manipulations, or via genetic improvement are on-going. If reduced aggression in new social groups is found to be detrimental to long-term group stability, then it will be important to quantify any continual welfare or production concerns that arise as a consequence of reducing mixing aggression. Although this study focuses on pigs due to the costs of aggression in this species, the existence of a trade-off between acute aggression at mixing and subsequent chronic aggression may have implications for other species reliant upon dominance relationships.

Many pig aggression studies use information taken from small group sizes or staged interactions between individuals. Often they focus on one aspect of aggression, for example the effects of body weight or previous fight success (Andersen et al. , 2000; Francis, Christisonl, & Cymbaluk, 1996) . This study utilises a dataset comprised of extremely detailed behavioural observations taken from more than 1,100 animals under commercially relevant conditions after 24 hours post mixing. This has provided an opportunity to study the behavioural repertoire of the pig when placed in an unstable social environment, with no human interference. These behavioural traits were compared to skin lesions at mixing (SL24h) and in the social stable group (SL3wk).

This study investigated whether there is a phenotypic link between aggression at mixing and increased long-term group stability in the form of reduced skin lesions, and if so, to identify mixing behaviours that improve long-term social behaviour. In particular it was of interest to identify specific behaviours associated with skin lesions at mixing and three weeks post mixing.

2. Methods

2.1. Animals and housing

The study comprised 1,166 pigs on a commercial farm in Ransta, Sweden, between October 2005 and January 2007. Information gathered on all individuals included pen identity, sex, breed, litter identity, and unique pig identification (ear tag or notch number). Single sex (intact males, castrated males, and females) and single breed (703 purebred Yorkshire and 463 crossbred Yorkshire x Landrace) groups of 15 were created by mixing 3 pigs from 5 different litters, resulting in 78 groups. Effort was made to standardise within-pen variation in body weight across groups. Animals were weighed 24 hours post-mixing and showed an average live weight of 27.6 kg (*SD* = 5.6) and an average age of 72 days (*SD* = 4.3). Pigs were housed in 4.0 x 3.2 m partially slatted pens (30% slats, 70% lightly bedded solid flooring) with a floor space allowance of 0.85 m^2 per pig. Pigs were fed dry pelleted food *ad libitum* from a single space feeder and had constant access to water via a nipple drinker.

2.2. Skin lesion traits

Lesions were counted immediately prior to mixing, and again 24 hours post-mixing by a single observer, and were grouped by location on the body: anterior (head, neck, front legs, and shoulders), central (flanks and back), posterior (rump, hind legs, and tail). The pre-mixing lesion count was subtracted from that taken 24 hours post-mixing for each pig. This served to ensure that only those lesions that occurred as a result of mixing aggression (SL24h) were included in all analyses. Recently received lesions were counted again three weeks post-mixing (89.8 days (SL3wk) [*SD* = 5.2]). One uninterrupted scratch was classed as a single lesion, regardless of length or severity. A lesion was considered to be recent if it was vivid red in colour or recently scabbed.

2.3. Behavioural traits

Groups were video recorded for 24 hours post-mixing. Time, duration (s), and outcome of reciprocal (RA) and non-reciprocal (NRA) aggression were recorded. Reciprocal aggression was defined as a fight that lasted more than one second where both pigs were involved in pushing, head knocking or biting. Non-reciprocal aggression involved the delivery of these behaviours with no retaliation from the receiver. Non-reciprocal aggression could occur as a unique event independent of a reciprocal fight, as a component of a reciprocal fight, or at the end of a reciprocal fight as the loser retreated. In addition, for each fight, observers recorded the duration of time spent engaged in injurious fighting. This is opposed to behaviour such as pushing, head knocking, or chasing, which were not deemed injurious. These basic data were used to derive quantitative aggressive behavioural traits that were used in the statistical analysis in the current study (Table 1). Three observers used time-lapse video equipment to extract the duration of each behavioural bout to the nearest second. Analysis of three 1-hour samples of data showed a significant degree of inter-observer agreement (r = 0.83, P < 0.001) (Turner et al. 2009).

2.4. Characteristics of the data

Skin lesion and behavioural data were available for all 1,166 animals in 78 groups. Animals were mixed with an average growth rate of 881 g/day over an 86 day (SD = 4) growth period (Yorkshire: 880 g/day [SD = 155]; Yorkshire x Landrace: 881 g/day [SD = 186]). The average weight of pigs at the time of mixing was 27 kg (Yorkshire: 27 kg [SD = 5.1]; Yorkshire x Landrace: 29 kg [SD = 5.4]) and the average weight at the end of the finishing period was 104 kg (Yorkshire: 103 kg [SD = 11.24]; Yorkshire x Landrace: 106 kg [SD = 12.49]). The characteristics of the data for the variables used in the analyses are presented in Table 2. Negative values for skin lesions at 24 hours post mixing are partly due to observer error and partly due to lesions healing between pre and post mixing lesion number counts. Within further analysis of the data, these negative values were set to zero. The lesion numbers and behavioural traits showed skewed distributions (Table 2); therefore the data were log transformed (y = ***LS*** + 1) and the transformed values were used in all subsequent analyses.

2.5. Statistical Analyses

To account for systematic influences on behavioural traits and skin lesions, the effects of breed type (purebred Yorkshire, Yorkshire × Landrace), sex (females, males, and castrates) and experimental batch (pigs were mixed on 14 separate days) were fitted as class variables, and body weight as a covariate in the statistical models. The group effect was modelled by including the pen in which the animals were mixed as random effect. The analysis was carried out using the MIXED procedure of SAS (version 9.1). To predict the individual animal associations and to identify the change in aggression of animals over time, Pearson correlations were obtained between the residuals of all behavioural traits and SL24h with SL3wks. Aggression is often discussed in terms of the individual animal, however pigs are housed in social groups, and the welfare of an individual is likely to be greatly affected by the level of social stability within the group in which it is housed. In order to compare group-level associations between behaviour and lesion numbers, correlations between estimates of pen effects were calculated.

To further explore the relationship between aggression at mixing and skin lesions for individual animals at two time points, a multiple linear regression model was developed that resulted in the best model to predict lesion numbers from a set of behavioural traits. A series of multiple stepwise regression analyses using the REG procedure of SAS (version 9.1) were performed, in which the estimated residuals for lesion and behavioural traits from the initial mixed models for SL24h and SL3wk were set as response variables, and residuals for all behavioural traits were set as predictors. Behaviour traits explaining significant variance in lesion numbers ($P < 0.05$), as predicted by the regression analyses, were included in the final model. Many behavioural traits may be correlated among each other; therefore multicollinearity between behavioural variables included in the final model was estimated using variance inflation factors (VIF); however no VIF were above 1.38, suggesting that multicollinearity was not a concern. Using residuals of behavioural traits, the final model produced regression coefficients that predicted how various behaviours influenced lesion numbers at both time points, independent of systematic effects described above.

3. Results

There were large variations among pen group means of SL24h, suggesting that groups differed significantly in levels of aggression. There was less variation among pen group means for SL3wk than SL24h. However the averages of all pen group means for SL24h were similar to SL3wk at the centre or posterior of the body but not for those observed at the anterior area (Table 3). The distribution of pen group means of skin lesions was approximately normal, as assessed by the skewness and kurtosis (Table 3), with the exception of posterior SL24h, which was slightly negatively skewed.

3.1. Fixed and random effects on skin lesions

Batch and breed type*sex were included in the mixed models as fixed class effects while body weight at mixing was included as a covariate. Batch effects were statistically significant for almost all lesion traits except for anterior and central SL24h (posterior SL24h: $F = 8.59$; $P < 0.001$; anterior SL3wk: $F = 5.25$, $P < 0.001$; central SL3wk: $F = 7.70$; $P <0.001$; posterior SL3wk: $F = 5.72$, $P < 0.001$). Breed type*sex affected anterior and central SL3wk (anterior $F = 5.25$; $P < 0.001$; central $F = 3.12$; $P = 0.014$). Cross bred females received significantly fewer anterior and central SL3wk ($P < 0.05$) than purebred females. Anterior and posterior SL24h showed significant regression coefficients ($P < 0.001$ and $P = 0.046$) on body weight at mixing.

3.2. Lesion numbers

The proportions of the phenotypic variance attributed to pen effects were significant ($P < 0.05$) in the range from 4 to 12% and 3 to 21% for skin lesions (on the diagonal of Table 4) and most behavioural traits, respectively (Table 5).

On the pen group level, lesions across body regions at the same time point were positively correlated (SL24h: 0.28 to 0.77; $P < 0.01$, SL3wk: 0.65 to 0.75; $P < 0.001$). Between time points, anterior or central pen group SL24h were positively correlated with anterior or central SL3wk (0.24 to 0.36; $P < 0.05$). Lesions to the central region of the body were also positively correlated on a pen group level across time points (0.24; $P < 0.05$) (above diagonal, Table 4).

At the individual animal level, lesions across body regions recorded at the same time point were positively correlated for both SL24h (0.38 to 0.54; $P < 0.001$), and SL3wk (0.50 to 0.65; $P < 0.001$). Between these time points, there were significant but small positive correlations between central (0.07; $P < 0.05$) or posterior (0.07; $P < 0.05$) SL24h and anterior SL3wk. In contrast, there was a small negative but significant correlation between anterior SL24h and central SL3wk (-0.06; $P < 0.05$) (below diagonal, Table 4).

3.3. Correlations between behavioural and lesion traits on group (pen) level

Between pen groups correlations of behavioural with lesion traits are presented in Table 5. The aggressive behavioural traits showed mostly significant positive correlations with SL24h (0.23 to 0.61; $P < 0.05$), except for the trait proportion of injurious fights, which was negatively correlated with the posterior region at 24 hours (-0.27; $P < 0.01$). In contrast, significant correlations of behavioural traits with SL3wk were consistently negative (-0.23 to -0.33; $P < 0.05$). Between pen groups, behavioural traits were primarily associated with skin lesions to the anterior regions of the body at 24 hours post-mixing, and to the central region of the body at 3 weeks post mixing. In addition, most significant correlations were found for behavioural traits that were defined as reciprocal aggression, with the exception of total non-reciprocal aggression received (0.24; $P < 0.05$) which positively correlated with the posterior SL24h, and duration of non-reciprocal aggression received, which positively correlated with central (0.23; $P < 0.05$) and posterior (0.23; $P < 0.05$) SL24h (Table 5). A summary of the main correlations found between pen groups is presented in Figure 1.

3.4. Correlations between behavioural and lesion traits on individual animal level

Under unstable social conditions at mixing, all behavioural traits included in the analysis showed positive correlations with anterior SL24h (0.13 to 0.56; $P < 0.001$) (Table 6). Except for the behavioural traits proportion of fights won, all other analysed behavioural traits were positively correlated with central SL24h (0.08 to 0.33; $P < 0.01$) but mostly at a lower magnitude than those of anterior lesions. Even lower correlations were calculated between behavioural traits and posterior SL24h (0.06 to 0.22; $P < 0.05$). The direction of these correlations indicates that individuals that are involved in more aggression at mixing received more SL24h, in particular to the anterior body region. A summary of the main correlations found on individual animal level is presented in Figure 2.

Many measures of aggressive behaviours at mixing correlated negatively with anterior and central SL3wk but at a lower magnitude than at those found at 24 hours (-0.07 to -0.18; $P < 0.05$). The behavioural traits number of RA involved with, the duration of RA and NRA initiated, and the average fight duration, showed the largest negative correlation with central SL3wk. The behavioural traits total NRA received, number of pen mates bullied by, and the proportion of fights with an ambiguous outcome were not associated with the number of anterior or central SL3wk. The duration of NRA received was negatively associated with central but not anterior or posterior SL3wk (Table 6).

3.5. Best model for prediction of lesion numbers

Of all skin lesion traits, anterior SL24h showed the highest predictability by behavioural traits of aggression (R^2 = 0.36) (Table 7). Central SL24h were affected by the highest number of behavioural traits. As found with the residual correlations, the regression model predicted a positive association between behavioural traits of aggression at mixing and SL24h, with the exception of the trait proportion of fights won, which was associated with slightly fewer central (P < 0.001) and posterior (P = 0.015) SL24h. At three weeks, only lesions to the central region of the body could be predicted by behavioural traits of aggression at mixing, however the R^2 value was low. The model predicted a negative association between traits of aggression, with the exception of the duration of NRA received, which was associated with slightly more SL3wk (P < 0.001) (Table 7).

Almost all behavioural traits included in all prediction models were significantly and positively correlated with each other (0.06 to 0.93; P < 0.05). The proportion of fights won was slightly negatively correlated with the total number of NRA received (-0.10; P < 0.001) and the duration of NRA received (-0.10; P < 0.001). There was no statistically significant correlation between the average duration of RA and NRA involved with and total number of NRA received (Table 8). However, highly correlated behavioural traits were not selected for each prediction model by the stepwise regression analysis so that multicollinearity was not a concern.

4. Discussion

4.1. Behaviour and skin lesions on group level

Aggression can be defined at the level of individuals or at a group level. Numbers of lesions have been previously validated as a method of measuring the aggressiveness of individual pigs at mixing (Turner et al., 2006[a]) but not as a measure of aggression across entire groups. The current data set was an ideal opportunity to study the group level basis to skin lesions. The direction of the correlations indicates that increased group level involvement in reciprocal aggression, involving more pen mates, resulted in higher average anterior SL24h. Pen level correlations between aggression and lesions at mixing suggest that skin lesions are a useful measure of reciprocal aggression at mixing within a group, but only for anterior regions, which have previously been linked to reciprocal aggression in individuals (Turner et al., 2008).

At the group level, behavioural variables that were positively associated with anterior SL24h were negatively associated with SL3wk; however this relationship was mainly significant for the central body region only. The vigorous, reciprocal aggression that accounts for many anterior lesions at mixing does not often occur in stable groups. Instead, aggression in stable groups is primarily seen in the form of head knocks and bites, often over a resource (Bolhuis et al., 2005), which could explain why a relationship was mainly found for the central region of the body.

Very few traits related to non-reciprocal aggression were associated with skin lesions on a group level, suggesting that skin lesions are not a useful measure of the amount of non-reciprocal aggression a group has been involved in. The majority of behaviour at mixing related to anterior SL24h on a group level, whereas lesions from non-reciprocal aggression are more likely to be inflicted to the centre and posterior region of the body as the recipient is often turned away from the attacker, as it attempts to escape. This is reflected in the group level correlations, as the number and duration of non-reciprocal aggression received were positively correlated with central and posterior SL24h.

If increased aggression at mixing increases social stability, it would be expected that SL3wks relates to the quality of aggression performed. For example if many fights within a group have definitive outcomes and are rarely repeated, the individuals involved might be more certain of their social position, resulting in a more stable hierarchy. There was little evidence of this in the current study, as skin lesions at SL3wk did not relate to the proportion of repeated fights, fight intensity or ambiguous outcomes at mixing. Groups with a high proportion of successful fights (proportion of fights won) tended to have low SL3wks. Correlations between behavioural traits (results not presented) indicate that groups with a high proportion of fights success also had a large number of unambiguous, intense fights. It is possible that social relationships are influenced by a combination of traits related to fight quality although individual traits do not correlate with skin lesions when considered in isolation.

Negative correlations between reciprocal aggression at mixing and SL3wk offer some support for the hypothesis that increased initial reciprocal aggression on a group level reduces aggression in the long term. Reduced aggression at three weeks could indicate a more stable social hierarchy. If this was the case, it could be that certain fighting experiences, in particular those related to reciprocal aggression, lead to less ambiguity over hierarchy positions, resulting in fewer conflicts over resources.

4.2. Behaviour and skin lesions on individual animal level

At the individual animal level, residual correlations between aggressive behavioural variables and SL24h indicate that an increase in almost all measures of aggression at mixing results in more skin lesions across all three body regions. Lesions to the anterior body region have previously been shown to be associated with reciprocal fighting, and the posterior and central regions of the body associated with receipt of non-reciprocal aggression (Turner et al., 2006[a]).

A multiple regression model was developed in the current study in order to further dissect the relationship between various aggressive strategies and the receipt of lesion numbers. As predicted by residual correlations, a general increase in aggression - for example long reciprocal fights - predicted higher lesions across all body regions 24h after mixing. Fight success (proportion of fights won) predicted fewer SL24h to central and posterior body regions when included in the model. This is likely to be because unsuccessful pigs receive more non-reciprocal aggression, resulting in slightly more lesions than their successful pen mates. Although the receipt of non-reciprocal aggression was weakly negatively correlated with fight success, the number and duration of non-reciprocal aggression received were positively associated with other measures of aggression, including the number of reciprocal interactions involved in and the number of pen mates bullied. Combined, these results suggest that while increased aggression of all descriptions increases the risk of receiving skin lesions, within this more aggressive cohort, the animals with a high fight success rate receive fewer skin lesions than their less successful but aggressive pen mates. Animals that avoid involvement in aggression altogether receive the lowest skin lesions at this time.

Correlations between aggressive behaviour at mixing and skin lesions recorded three weeks post-mixing were lower than those calculated for skin lesions 24 hours post mixing. As described earlier, aggression at mixing and in established groups tends to differ in its form and motivation, lacking the intense reciprocal aggression that constitutes the majority of aggressive behaviour at mixing (Bolhuis et al., 2005; Fraser, 1984). A strong correlation between the two traits was therefore not to be expected. Despite this, many measures of aggression were negatively correlated with SL3wk, indicating that the more aggression an individual is involved in at mixing, the fewer lesions it receives under stable social conditions, particularly to the anterior and central regions of the body. As found for associations with SL24h, behavioural correlations with the posterior region of the body 3 weeks post mixing were lower than those obtained for the anterior and central regions, resulting in extremely low correlations for this body region at that time point. This pattern indicates that posterior lesions are not as informative as lesions to the anterior body region. This may be because lesions are typically inflicted to the rear of the body during the receipt of aggression, and are therefore not a reflection of an individual's own behaviour, but rather that of its pen mates.

Behavioural traits accounted for very little variation in SL3wk, as predicted by the multiple regression models. The models predicted that the proportion of fights won at mixing accounted for most of the variation in central SL3wk, with the most successful animals receiving the fewest lesions at this time. This implies that skin lesions in stable groups are chiefly related to dominance, as it is likely that the most successful animals at mixing go on to achieve the highest-ranking positions in stable groups. As reflected by the correlations on individual animal level, the model predicted that an increase in the duration of non-reciprocal attacks received at mixing was associated with slightly increased central SL3wk. The duration of non-reciprocal attacks received was positively correlated with number and duration of non-reciprocal attacks initiated, and the duration of reciprocal aggression involved in. Therefore the animals that received much aggression were also actively involved in aggression. This finding reflects those found in a previous study involving a different population (Turner et al., 2006[a]). These results demonstrate that non-reciprocal aggression at mixing is not received by the unaggressive individuals in a group, but rather aggressive but unsuccessful animals, possibly as a means to reinforce a fight outcome.

The results from the correlations and mixed model predictions indicate that while high fight success at mixing results in the lowest stable lesions, involvement in aggression at mixing, even when unsuccessful, leads to fewer lesions in the stable group than animals which avoid aggression at mixing altogether. The simplest explanation is that pigs which avoid aggression are simply the most subordinate individuals; however this does not explain the observations made on a pen group level. It could be that simply engaging in aggression leads to less ambiguity over social standing, resulting in fewer challenges to hierarchy positions. Alternatively, it is possible that experience in physical aggression is necessary in learning to convey both dominant and submissive behaviours. Studies involving repeated mixing of pigs (Coutellier et al., 2007; Giersing & Andersson, 1998) have shown that the amount of aggression displayed reduces with increased mixing, whereas D'Eath (2005) found that early socialising of piglets leads to faster hierarchy formation. Frischknecht et al., (1982) demonstrated how mice that had experience of being defeated displayed significantly more submissive behaviours than those that had never experienced agonistic interactions. In the present study, pen group lesions at three weeks were negatively associated with traits related to reciprocal fighting. If important social skills are learned via fighting experience, this may explain why we see more social stability in groups that involved more reciprocal aggression between more group members.

Social instability in the form of long-term aggression may be caused by several factors. It is possible that groups with increased aggression 3 weeks post mixing have a less stable hierarchy than other groups, and therefore frequent physical aggression is required in order to re-establish or maintain dominance relationships. Alternatively, it may be that some individuals fail to recognise dominance relationships, or continue to fight at inappropriate times. As no behavioural data were available three weeks post-mixing, the stability of dominance relationships could not be assessed. As such, it is impossible to deduce whether long-term social instability was the result of unstable dominance relationships or socially dysfunctional individuals within a group.

The results of these analyses confirm that skin lesions are a useful alternative measure of aggressiveness displayed by individual pigs in the first 24 hours post mixing. While increased aggression at mixing leads to more injuries at first, it may be beneficial for the individual in the long term, even if the animal is not successful at fighting.

4.3. Lesion correlations

Lesions across body regions at the same time point were positively correlated meaning that animals that received high lesions to one region of the body were likely to receive lesions to other body regions. This is in accordance with the findings from the behavioural data in which animals that engage in a high amount of aggression of any form receive many lesions to all body regions.

Individuals that received high central and posterior SL24h were also somewhat likely to receive high anterior and central SL3wk, although the correlations were of a very low magnitude. These results appear to conflict with the direction of the correlations between aggression at mixing and SL3wk. Although this seems counterintuitive at first, the correlations between skin lesion traits are low, and contradicting correlations can occur due to the various effects that influence the correlations. It can be hypothesised that the contradictory relationship between aggressive behaviour and lesions at different time points may contribute to the reduced correlations between lesions at mixing and the stable group.

Genetic correlations using the same population showed a moderate to strong positive correlation between SL24h and SL3wk (Turner, 2009); however the same study also found negative residual correlations between these traits. This relationship was also observed on a group level, although the correlations were of a higher magnitude than those observed for individuals.

5. Conclusions

Research into reducing aggression via a combination of genetic and management strategies are on-going. Phenotypic correlations such as those explored in the present study offer some evidence that within groups of mixed aggression levels, increased reciprocal aggression may be beneficial to long term group dynamics. It may prove challenging to identify any single management strategy that will simultaneously reduce both mixing-induced aggression and on-going chronic aggression. In contrast, genetic correlations (Turner et al., 2009) and experiments in which animals were grouped according to aggressive personalities (Erhard et al., 1997) support the theory that reducing the level of aggression displayed by individuals may result in reduced long term aggression. The environment (O'Connell & Beattie, 1999), group size (Andersen et al, 2004; Hemsworth et al., 2014), genetics (Canario et al., 2012; Turner et al., 2006[b]; Turner et al., 2009), early life experience (D'Eath, 2005) and prenatal stress (Jarvis et al., 2006) have all been shown to affect social aggression in pigs. Further work is clearly required to disentangle these factors in order to better predict the possible consequences on aggression. In terms of genetic strategies to control aggression in pigs, this study raises the interesting question that selection for reduced aggression at mixing could result in increased levels of chronic aggression. Further studies should seek to calculate the genetic correlation between metrics of aggression at mixing and then during the stable state to uncover the genetic architecture of these two distinct traits.

The current study cannot address the question of whether skin lesions at three weeks not only relate to aggression, but that increased aggression in stable groups translates to poor welfare. Published studies examining the long term effects of social stress (usually by measuring cortisol or immune responses) have produced conflicting results (Blanchard et al., 1993; Mendl et al., 1992; Tuchscherer et al., 1998; Ekkel et al., 1997). In the present study, SL3wk were similar in number to SL24h for central and posterior lesions, indicating a comparable level of aggression at the two time points. It could be argued that dominance relationships are a part of the pig's natural behaviour and therefore individuals should be equipped to deal with the stress that arises from these encounters. However in space-restricted pens animals are often unable to adequately avoid persistent attacks (Fraser et al., 1995).

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Tables

Table 1. Definitions of skin lesion traits and behavioural traits used in the analyses

Trait	Description
Skin lesions at 24 hours (SL24h)	Number of skin lesions counted 24 hours post mixing
Skin lesions at three weeks (SL3wk)	Number of skin lesions counted 3 weeks post mixing (stable groups)
Reciprocal aggression (RA)	A fight lasting >1s in which the recipient of the attack retaliated
Non-reciprocal aggression (NRA)	An attack in which the recipient did not retaliate
RA involved with	Total number of reciprocal fights the focal pig was involved with, regardless of which pig initiated the attack
NRA involved with	Total number of non-reciprocal fights the focal pig was involved with, regardless of which pig initiated the attack
Total RA initiated/received	The total number of times an individual initiated or was the recipient of an attack which was reciprocated
Total NRA initiated/received	The total number of times an individual initiated or was the recipient of an attack which was not-reciprocated
Number of pen mates focal pig attacked (RA)	The number of pen mates the focal pig attacked in which the attack was reciprocated
Number of pigs attacked by (RA)	The number of pen mates the focal pig was attacked by which the focal pig retaliated against
Number of pen mates focal pig bullied	The number of pen mates the focal pig attacked which did not reciprocate
Number of pen mates bullied by	The number of pen mates the focal pig was attacked by which it did not reciprocate against

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Trait	Description
Pen mates involved with	Total number of pen mates with which the focal pig had any aggressive interactions
Average duration RA & NRA involved (s)	Average duration of all aggressive encounters in which the focal pig was involved
Duration of RA initiated (s)	Duration of time spent in RA in which the focal pig was the initiator
Duration of RA received (s)	Duration of time spent in RA in which the focal pig was the recipient of the attack
Duration of NRA initiated (s)	Duration of time spent in NRA in which the focal pig was the initiator
Duration of NRA received (s)	Duration of time spent in NRA in which the focal pig was the recipient of the attack
Proportion of fights won	Proportion of all reciprocal fights which the focal pig won
Proportion of repeated fights	Proportion of all pen mates fought with which the focal pig had more than one aggressive interaction
Proportion with ambiguous outcome	Proportion of reciprocal fights the focal pig was involved with in which the winner could not be determined
Proportion injurious RA involved with	Proportion of time the focal pig spent in reciprocal fights engaged in what was deemed to be injurious fighting

Table 2. Characteristics of behavioural and skin lesion data for individual animals included in the statistical analysis (SK = skewness; K = kurtosis)

	Original scale					Log transformed scale			
Trait	***N***	***Min-Max***	***Mean (SD)***	***SK***	***K***	***Mean***	***SD***	***SK***	***K***
Anterior SL24h	1166	-17 to 99	18.84 (17.32)	1.38	2.31	2.56	1.09	-0.88	0.34
Central SL24h	1166	-30 to 100	10.71 (12.02)	1.42	5.99	2.05	1.10	-0.63	-0.55
Posterior SL24h	1166	-42 to 41	3.70 (8.26)	-0.72	4.12	1.36	1.02	-0.11	-1.30
Anterior SL3wk	1166	0 - 63	10.4 (5.63)	1.57	8.67	2.30	-1.13	-1.13	2.60
Central SL3wk	1166	0 - 40	10.35 (5.94)	1.03	1.86	2.28	0.6	-0.93	1.58
Posterior SL3wk	1166	0 - 30	4.51 (3.51)	1.21	3.07	1.48	0.71	-0.51	-0.35
RA involved with	1166	0 - 56	8.36 (7.14)	1.37	3.05	1.90	0.90	-0.58	-0.38
NRA involved with	1166	0 - 69	7.65 (6.95)	2.86	15.27	1.89	0.75	-0.29	0.23
Total RA initiated	1166	0 - 36	4.19 (4.29)	1.76	4.99	1.32	0.85	-0.13	-0.90
Total RA received	1166	0 - 25	4.17 (3.77)	1.44	3.06	1.36	0.79	-0.31	-0.74
Total NRA initiated	1166	0 - 66	3.84 (5.54)	3.84	25.9	1.14	0.91	0.33	-0.70
Total NRA received	1166	0 - 25	3.81 (3.17)	1.57	3.89	1.36	0.67	-0.26	-0.28
Number of pen mates focal pig attacked (RA)	1166	0 - 11	2.84 (2.32)	0.66	-0.19	1.13	0.69	-0.38	-0.96
Number of pigs attacked by (RA)	1166	0 - 9	2.84 (2.06)	2.06	-0.52	1.17	0.64	-0.57	-0.69
Number of pen mates focal pig bullied	1166	0 - 14	2.56 (2.68)	1.32	1.55	0.99	0.75	0.06	-1.10
Number of pen mates focal pig bullied by	1166	0 - 9	2.56 (1.67)	1.67	0.09	1.15	0.52	-0.56	-0.10
Pen mates involved with	1166	0 - 14	6.67 (3.06)	0.02	-0.67	1.94	0.49	-1.12	1.43
Average duration of NA & NRA involved (s)	1159	1 - 249	42.48 (27.82)	2.04	8.33	3.58	0.64	-0.38	0.45
Duration of RA initiated	1166	0 - 2394	286.26 (364.26)	2.09	5.41	4.27	2.34	-0.87	-0.56
Duration of RA received	1166	0 - 2997	326.45 (351.62)	2.09	6.68	5.08	1.46	-1.09	1.49
Duration of NRA received	1166	0 - 996	41.61 (68.46)	2.87	13.79	3.11	1.34	-0.88	0.32
Duration of NRA initiated	1166	0 - 444	41.29 (46.46)	4.63	40.84	2.52	1.82	-0.19	-1.27
Proportion of fights won	1066	0 - 1	0.30 (0.25)	0.57	-0.22	0.25	0.19	0.22	-0.82
Proportion of repeated fights	1159	0 - 1	0.50 (0.25)	-0.34	-0.35	0.39	0.18	-0.74	0.02
Proportion with ambiguous outcome	1066	0 - 1	0.27 (0.24)	0.87	0.67	0.22	0.18	0.44	-0.37
Proportion injurious	1156	0 - 1	0.59 (0.24)	-1.07	0.76	0.45	0.17	-1.46	1.66

Table 3. Variations between 10% lowest and highest in pen group means for lesion numbers. (SL24h = lesion numbers at 24 hours post mixing, SL3wk = lesion numbers 3 weeks post mixing. SK = skewness, K = kurtosis).

Trait	Lowest 10% in group means	Average over all group means (*SD*)	Highest 10 % in group means	SK	K
SL24h					
Anterior	8.07	18.82 (6.65)	32.68	0.80	2.54
Central	2.91	10.71 (5.39)	21.43	0.70	-0.09
Posterior	-9.66	3.69 (5.79)	10.87	-1.91	4.93
SL3wk					
Anterior	6.77	10.40 (2.21)	14.34	-0.53	0.02
Central	6.28	10.34 (2.58)	15.37	-0.64	0.86
Posterior	1.79	4.51 (1.62)	7.46	-0.85	0.86

Table 4. Phenotypic proportions of skin lesion number (SL) variance attributable to pen group effects (on diagonal in bold) and the correlation between pen group effects (above diagonal), and individual animal (residual[a]) correlations (below diagonal) between lesion numbers recorded 24 hours post mixing and three weeks post mixing.

	SL24h			SL3wk		
Trait	Anterior	Central	Posterior	Anterior	Central	Posterior
SL24h						
Anterior	***0.08 *****	0.45 ***	0.28 **	-0.07	-0.09	0.06
Central	0.53 ***	***0.11 ******	0.77 ***	0.20	0.24 *	0.11
Posterior	0.38 ***	0.54 ***	***0.12 ******	0.36 ***	0.32 **	0.19
SL3wk						
Anterior	-0.00	0.07 *	0.07 *	***0.04 ****	0.65 ***	0.69 ***
Central	-0.06 *	0.00	0.01	0.65 ***	***0.09 ******	0.75 ***
Posterior	-0.02	0.01	0.04	0.50 ***	0.58 ***	***0.07 *****

[a] Residual correlation after accounting for all systematic effects and the group (pen) effects.

**P* < 0.05, ***P* < 0.01, ****P* < 0.001.

Table 5. Phenotypic proportions of behavioural variance attributed to pen group effects (column 1), and correlations of estimates of pen group effects between aggressive behaviour and skin lesion numbers recorded 24 hours (SL24h) and 3 weeks (SL3wk) post-mixing.

Trait	Proportion of pen	SL24h Anterior	SL24h Central	SL24h Posterior	SL3wk Anterior	SL3wk Central	SL3wk Posterior
RA involved with	0.10 ***	0.61 ***	-0.04	-0.19	-0.21	-0.33 **	-0.10
NRA involved with	0.21 ***	0.09	0.14	0.16	0.03	-0.11	-0.10
Total RA initiated	0.06 **	0.59 ***	-0.01	-0.17	-0.23 *	-0.32 **	-0.10
Total RA received	0.10 ***	0.63 ***	-0.03	-0.18	-0.22	-0.33 **	-0.09
Total NRA initiated	0.04 *	0.21	0.08	0.08	-0.06	-0.20	-0.15
Total NRA received	0.20 ***	0.07	0.22	0.24 *	0.10	-0.01	-0.05
Number of pen mates attacked (RA)	0.07 **	0.58 ***	-0.04	-0.17	-0.21	-0.30 **	-0.08
Number of pigs attacked by (RA)	0.10 ***	0.60 ***	-0.07	-0.18	-0.20	-0.30 **	-0.07
Number of pen mates focal pig bullied	0.03 *	0.23 *	0.08	0.08	-0.10	-0.21	-0.21
Number of pen mates bullied by	0.15 ***	0.12	0.22	0.21	0.02	-0.05	-0.13
Pen mates involved with	0.12 ***	0.41 ***	0.06	0.02	-0.14	-0.26 *	-0.20
Average duration of RA & NRA involved (s)	0.17 ***	0.37 ***	0.03	-0.08	-0.18	-0.14	-0.11
Duration of RA initiated (s)	0.05 **	0.55 ***	0.01	-0.12	-0.18	-0.26 *	-0.06
Duration of RA received (s)	0.08 **	0.57 ***	0.10	0.01	-0.24 *	-0.24 *	-0.14
Duration of NRA initiated (s)	0.03	0.21	0.08	0.07	-0.10	-0.21	-0.23 *
Duration of NRA received (s)	0.13 ***	0.07	0.23 *	0.23 *	0.07	0.01	-0.10
Proportion of fights won	0.03	0.23 *	-0.13	-0.18	-0.24 *	-0.28 **	-0.11
Proportion of repeated fights	0.05 **	0.23 *	-0.01	-0.07	-0.10	-0.15	0.01
Proportion with ambiguous outcome	0.11 ***	0.00	0.01	0.06	0.13	0.08	0.02
Proportion injurious	0.07 **	0.37 ***	-0.14	-0.27 **	-0.12	-0.09	0.10

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Table 6. Correlations[(a)] between estimates of aggressive behaviour and skin lesion numbers recorded 24 hours (SL24h) and 3 weeks (SL3wk) post-mixing at the individual animal level.

		SL24h			SL3wk	
Trait	Anterior	Central	Posterior	Anterior	Central	Posterior
RA involved with	0.56 ***	0.32 ***	0.20 ***	-0.14 ***	-0.18 ***	-0.08 **
NRA involved with	0.34 ***	0.25 ***	0.15 ***	-0.09 **	-0.09 **	-0.05
Total RA initiated	0.43 ***	0.22 ***	0.13 ***	-0.12 ***	-0.14 ***	-0.05
Total RA received	0.48 ***	0.29 ***	0.17 ***	-0.10 ***	-0.16 ***	-0.08 **
Total NRA initiated	0.28 ***	0.17 ***	0.08 **	-0.12 ***	-0.15 ***	-0.07 *
Total NRA received	0.18 ***	0.20 ***	0.18 ***	0.03	0.05	0.00
Number of pigs attacked (RA)	0.50 ***	0.32 ***	0.20 ***	-0.11 ***	-0.15 ***	-0.09 **
Number of pigs attacked by (RA)	0.50 ***	0.32 ***	0.20 ***	-0.11 ***	-0.15 ***	-0.09 **
Number of pen mates focal pig bullied	0.30 ***	0.19 ***	0.09 **	-0.12 ***	-0.16 ***	-0.08 **
Number of pen mates bullied by	0.21 ***	0.20 ***	0.17 ***	0.03	0.04	-0.02
Pen mates involved with	0.48 ***	0.29 ***	0.17 ***	-0.14 ***	-0.15 ***	-0.09 **
Average duration of RA & NRA involved (s)	0.48 ***	0.23 ***	0.18 ***	-0.07 *	-0.12 ***	-0.09 **
Duration of RA initiated (s)	0.49 ***	0.23 ***	0.14 ***	-0.14 ***	-0.17 ***	-0.07 **
Duration of RA received (s)	0.54 ***	0.33 ***	0.22 ***	-0.10 ***	-0.14 ***	-0.10 ***
Duration of NRA initiated (s)	0.29 ***	0.17 ***	0.10 ***	-0.12 ***	-0.17 ***	-0.09 **
Duration of NRA received (s)	0.23 ***	0.22 ***	0.21 ***	0.04	0.08 **	0.00
Proportion of fights won	0.13 ***	-0.05	-0.07 *	-0.12 ***	-0.13 ***	-0.05
Proportion of repeated fights	0.35 ***	0.21 ***	0.16 ***	-0.08 **	-0.08 **	-0.04
Proportion with ambiguous outcome	0.18 ***	0.08 **	0.06 *	0.03	-0.01	0.00
Proportion injurious	0.30 ***	0.12 ***	0.08 **	-0.12 ***	-0.13 ***	-0.03

[a] Residual correlation after accounting for all systematic effects and the group (pen) effects.

P* < 0.05, ** *P* < 0.01, * *P* < 0.001

Table 7. Regression model predicting skin lesions recorded 24 hours (SL24h) and 3 weeks (SL3wk) post-mixing from aggressive behavioural traits based on the individual animal information

Skin lesions predicted by	*P* Value	Regression coefficient (SE)	Cumulative R^2 (a)
SL24h			
Anterior			
RA involved with	<0.001	0.47 (0.04)	0.30
Average duration of RA & NRA involved (s)	<0.001	0.53 (0.05)	0.35
Total NRA received	<0.001	0.21 (0.04)	0.36
Central			
Number of pigs attacked by (RA)	<0.001	0.34 (0.07)	0.08
Total NRA received	<0.001	0.30 (0.05)	0.10
Average duration of RA & NRA involved (s)	<0.001	0.32 (0.06)	0.12
Proportion of fights won	0.001	-0.69 (0.17)	0.13
Number of pen mates focal pig bullied	0.002	0.15 (0.05)	0.13
Posterior			
Duration of NRA received (s)	<0.001	0.11 (0.02)	0.04
Average duration of RA & NRA involved (s)	<0.001	0.17 (0.06)	0.05
Proportion of fights won	0.015	-0.51 (0.15)	0.06
RA involved with	<0.001	0.15 (0.04)	0.07
SL3wk			
Central			
Duration of NRA initiated (s)	<0.001	-0.04 (0.01)	0.02
Duration of NRA received (s)	<0.001	0.05 (0.01)	0.03
Average duration of RA & NRA	<0.001	-0.11 (0.03)	0.04
Proportion of fights won	0.044	-0.20 (0.10)	0.05

[a] *For each body region, cumulative R^2 values represent the proportion of the total phenotypic variance explained by the corresponding predictor in addition to predictors listed in previous rows of the table.*

Table 8. Residual correlations between estimates of aggressive behaviours included in final models, as presented in Table 7

	Trait	**b**	**c**	**d**	**e**	**f**	**g**	**h**
a	RA involved with	0.52 ***	0.19 ***	0.84 ***	0.37 ***	0.65 ***	0.19 ***	0.61 ***
b	Average duration of RA & NRA involved (s)		0.01	0.46 ***	0.20 ***	0.14 ***	0.13 ***	0.16 ***
c	Total NRA received			0.16 ***	-0.10 ***	0.06 *	0.88 ***	0.07 **
d	Number of pigs attacked by (RA)				0.18 ***	0.49 ***	0.17 ***	0.46 ***
e	Proportion of fights won					0.32 ***	-0.10 ***	0.29 ***
f	Number of pen mates focal pig bullied						0.07 *	0.93 ***
g	Duration of NRA received (s)							0.07 *
h	Duration of NRA initiated (s)							

*$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$